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## THE INTERCEREBRALIS-CARDIACUM-ALLATUM SYSTEM OF SOME PLECOPTERA<sup>1</sup>

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In spite of the interesting taxonomic position of the Plecoptera and the biological peculiarities of these insects their endocrine glands have been studied only by a small number of investigators. The existence of corpora allata in *Perla maxima* Scop. was first reported by Nabert (1913). In *Nemura vallicularia*, Wu (1923) described "lateral ganglia" which perhaps correspond to the corpora cardiaca. Hanström (1940) gave the first exact description of the endocrine glands in four species of Plecoptera (*Nemura variegata* Oliv., *Chloroperla viridis* Zett., *Isopteryx burmeisteri* Pictet, and *Perla cephalotes* Curt.). He showed that the anatomy of the endocrine glands of *Nemura* differs greatly from that of the three other species. In *Nemura* the medially located corpora cardiaca are fused with an unpaired lateral corpus allatum, while the three other species possess symmetrical paired corpora allata which are connected with the corpora cardiaca by anatomically defined nervi corporis allati. Histologically, according to Hanström, the corpora cardiaca of the Plecoptera contain cells whose general appearance is that of neurons but whose glandular function seems probable on account of the presence of fuchsinophilic secretory granules. Likewise, the glandular function of the corpora allata is indicated by the occurrence of acidophilic secretory granules. Regarding the innervation of these endocrine glands, Hanström found, in the four species of Plecoptera studied, the two pairs of protocerebral nerves whose existence he had demonstrated in other Pterygota, and indicated that their cells of origin have the same location as in other insects. No new data have been added to this description in the general survey on the subject by Cazal (1948).

This brief summary indicates that the endocrine glands in the head region of the Plecoptera are only incompletely known. The study of a larger number of species seems desirable because of the pronounced anatomical differences in the representatives of this order studied by Hanström (1940). Furthermore, none of the papers quoted above contain any information on two important histophysiological problems recently brought to light, *i.e.*, the relationships of the endocrine glands with the

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neurosecretory cells, and the changes which these glands undergo in the course of post-embryonic development.

We have, therefore, undertaken a study of the endocrine glands of the head region in representatives of seven families of the Plecoptera of the European fauna.<sup>2</sup> In the present paper we shall report new data regarding the "organ system" formed by the neurosecretory cells of the pars intercerebralis, the corpora cardiaca and the corpora allata (Scharrer and Scharrer, 1944; B. Scharrer, 1952).

#### MATERIAL AND METHODS

We were able to examine numerous specimens, in different stages of post-embryonic development, belonging to the following species (classification and nomenclature according to Aubert, 1946) :

Perlodidae	<i>Perlodes intricata</i> Pict. <i>Perlodes mortoni</i> Klap. <i>Isogenus alpinus</i> Pict. <i>Isogenus fontium</i> Ris.
Perlidae	<i>Perla maxima</i> Scop. <i>Perla marginata</i> Panz. <i>Perla cephalotes</i> Curt. <i>Perla carlukiana</i> Klap.
Chloroperlidae	<i>Isoperla grammatica</i> Scop. <i>Isoperla rizulorum</i> Pict.
Taeniopterygidae	<i>Brachyptera risi</i> Morton <i>Rhabdiopteryx alpina</i> Küht.
Capniidae	<i>Capnioneura nemuroides</i> Ris.
Leuctridae	<i>Leuctra hippopus</i> Kemp. <i>Leuctra inermis</i> Kemp.
Nemuridae	<i>Nemura mortoni</i> Ris. <i>Nemura marginata</i> Ris. <i>Nemura intricata</i> Ris. <i>Nemura praecox</i> Morton <i>Nemura nimborum</i> Ris. <i>Nemura lateralis</i> Ris.

The tissues were fixed in Bouin, Duboscq-Brazil, or Carnoy. The material was embedded in celloidin-paraffin and cut serially at 5 and 7  $\mu$ . Among stains for general survey we have used especially hemalum-picroindigocarmin, the triple stain of Prenant (as modified by Gabe and Prenant, 1949), and azan. The neurosecretory cells can be well demonstrated with the latter method, but the study of the migration of the neurosecretory product along the axons is greatly facilitated by the use of the chrome hematoxylin-phloxine method of Gomori (1941). Furthermore, we have employed the method of Brachet for the histochemical determination of ribonucleic acid, the method of Hotchkiss-McManus for the demonstration of polysaccharides, and Best's carmine stain with the saliva test for glycogen.

<sup>2</sup> We are obliged to Dr. J. Aubert, Musée zoologique, Lausanne, Switzerland, and to Dr. T. T. Macan, Ambleside, Westmorland, England, for supplying us with well preserved material.

## RESULTS

The information regarding the intercerebralis-cardiacum-allatum system of the Plecoptera obtained in the present study concerns (a) the anatomy of the endocrine glands, (b) the relationships of these glands with the neurosecretory cells, and (c) the development of these glands of internal secretion in the course of post-embryonic life.

### 1. Anatomy of the endocrine glands of the head region

It is known since the work of Hanström (1940) that certain Plecoptera have paired symmetrical corpora allata, while others have an unpaired lateral corpus allatum. To these two we can add a third type, characterized by a median unpaired corpus allatum (Arvy and Gabe, 1953b).

(a) *Type: Chloroperla*. Under this category Hanström classifies animals which are characterized by the existence of paired corpora allata, i.e. *Chloroperla virens*, *Isopteryx burmeisteri* and *Perla cephalotes*. The examination of a more extensive material permits us to state that the classification of Hanström is valid for all Perlodidae, Perlidae, and Chloroperlidae which we were able to examine.

In all representatives of this type the corpora cardiaca are fused in the midline and surround the dorsal vessel; they receive two pairs of nerves from the protocerebrum, the nervi corporis cardiaci I and II, whose cells of origin lie in the pars intercerebralis and next to the corpora pedunculata. The corpora cardiaca give rise to two nervi corporis allati which are rather short, but thick. The ventral portion of the corpora cardiaca is fused with the hypocerebral ganglion which re-

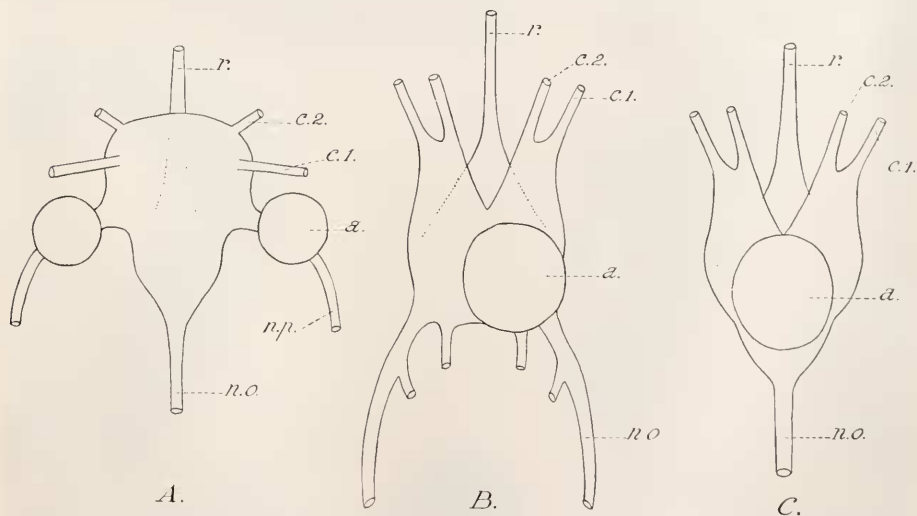
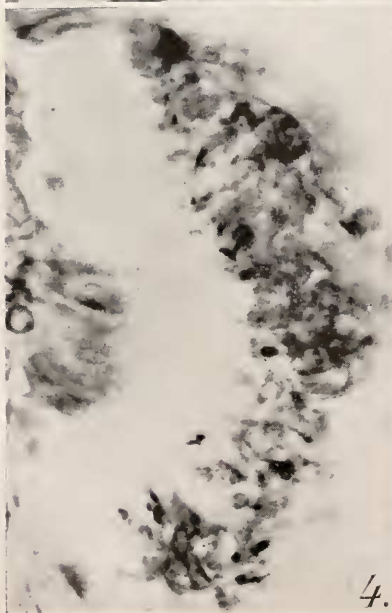
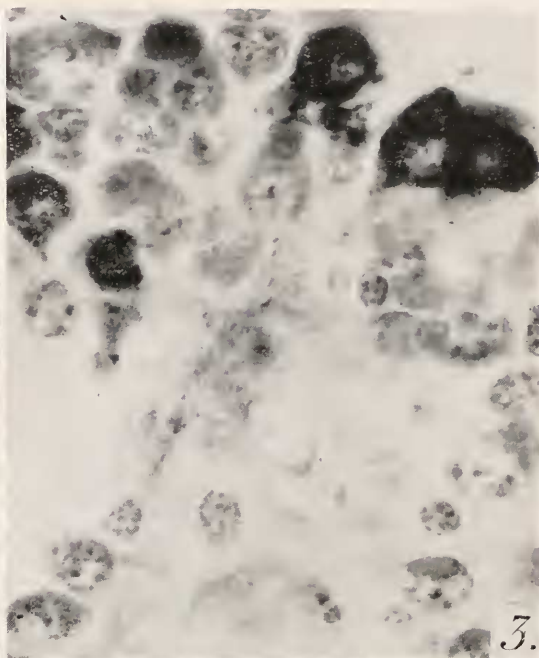
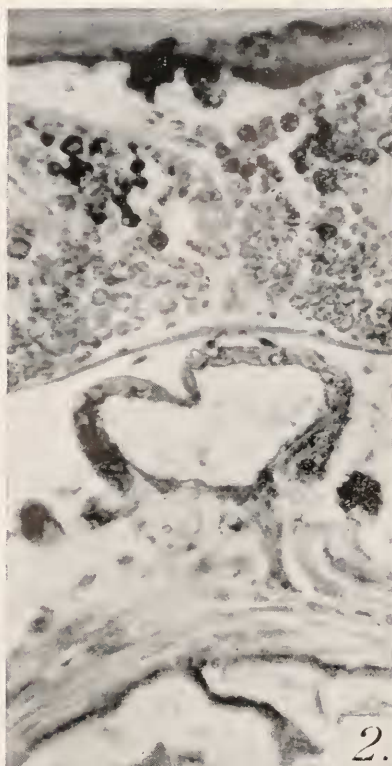


FIGURE 1. Diagrams of the three anatomical types of the retrocerebral glandular complex in the Plecoptera. A. Type of *Chloroperla* (according to Hanström, 1940), found in Perlodidae, Perlidae, and Chloroperlidae; B. Type of *Nemura* (according to Hanström, 1940), found in Capniidae, Leuctridae, and Nemuridae; C. Type of Brachyptera (according to Arvy and Gabe, 1953b), found in Taeniopterygidae. a., corpus allatum; c.1., nervus corporis cardiaci I; c.2., nervus corporis cardiaci II; n.o., esophageal nerve; n.p., prothoracic nerve; r., recurrent nerve.



FIGURES 2-5.

ceives the recurrent nerve and sends off the median unpaired esophageal nerve. From each corpus allatum a good-sized nerve originates which traverses the posterior part of the head, receives a branch from the connective which links the subesophageal and the prothoracic ganglia and branches in the prothorax (Figs. 1A, 10).

(b) *Type: Nemura*. The anatomy of the endocrine glands of the head of *Nemura variegata* is quite different (Hanström, 1940). According to our studies this type of organization also applies to the Capniidae, the Leuctridae and the Nemuridae. The corpora cardiaca, fused in the midline, also in this group receive the same nerves from the protocerebrum as those of the insects of the Chloroperla type. The unpaired corpus allatum lies asymmetrically at the right side and is intimately connected with the fused part of the corpora cardiaca and the hypocerebral ganglion. There are no anatomically defined nervi corporis allati. From the posterior end of this organ complex arise two esophageal nerves which supply the stomodaeum (Fig. 1B).

(c) *Type: Brachyptera*. This type was found only in representatives of the Taeniopterygidae and resembles that of *Nemura* with which it has in common the anatomy of the corpora cardiaca which are fused in the midline and receive the same innervation from the protocerebrum. The corpus allatum is unpaired but lies exactly medially (Fig. 2). As in *Nemura*, it is fused with the corpora cardiaca and the hypocerebral ganglion. The esophageal nerve arising from the caudal extremity of this organ complex is unpaired and median (Fig. 1C).

## II. Relationships between the endocrine glands and the neurosecretory cells

The morphological peculiarities of the cells of origin of the nervi corporis cardiaci I of the Plecoptera are known from the work of Hanström (1940). This author emphasizes the acidophilia of the cytoplasm of these cells, compares them with the elements of the same type which give rise to the nervi corporis cardiaci I in the Palaeoptera, and homologizes them with the paired frontal organs of the Apterygota. These cells possess all the morphological attributes of the neurosecretory cell as defined by Scharrer (for the bibliography see Scharrer and Scharrer, 1954). They elaborate an acidophilic product which stains with iron hematoxylin, with azocarmin and with chrome hematoxylin (method of Gomori). The secretory product passes along the axons arising from these cells. The course of the fibers can be followed with particular ease in preparations stained with chrome hematoxylin-phloxine. Comparable in their major outlines to the course

FIGURE 2. Section through caudal portion of cerebral ganglion, showing also corpora cardiaca (in center) and nervi corporis cardiaci I, in a larva of *Perla carlukiana*. Bouin, chrome hematoxylin-phloxine,  $\times 250$ . Note neurosecretory cells and accumulation of neurosecretory product in the corpora cardiaca and their nerves.

FIGURE 3. Neurosecretory cells in the pars intercerebralis of a larva of *Perlodes mortoni*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Note abundance of neurosecretory product in the cells and granules of the same material along the axons.

FIGURE 4. Frontal section through fused portion of corpora cardiaca in a larva of medium age of *Brachyptera risi*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Accumulation of neurosecretory product between the cells.

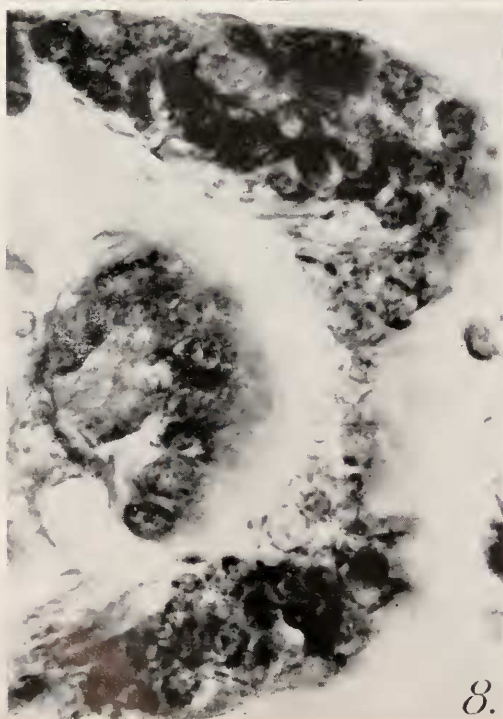
FIGURE 5. Detail from Figure 2,  $\times 1000$ . Accumulation of neurosecretory product in nervus corporis cardiaci I (bottom, left) and in corpus cardiacum.



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FIGURES 6-9.

of the nervi corporis cardiaci I of the Palaeoptera, the corresponding nerves in the Plecoptera show certain peculiarities in their anatomy. The cells of origin occupy a caudal position (Fig. 2), and the nervi corporis cardiaci I which cross the midline in the anterior portion of the protocerebrum leave the cerebral ganglia shortly after the decussation so that they accomplish a relatively long extraganglionic course on the ventral surface of the cerebral ganglion before entering the corpora cardiaca. The techniques used show in the intraganglionic portion of the nervi corporis cardiaci I very fine granules along the axons (Fig. 3). The extraganglionic portion of the nerves is much richer in secretory products, which accumulate markedly at the point where the nervi corporis cardiaci I change their course (Figs. 2, 5 and 6). In representatives of the type of *Chloroperla* the neurosecretory material appears in form of elongated and knotty masses, of big granules and droplets. This accumulation of the neurosecretory product where the fiber bundles arising from neurosecretory cells change their direction represents a rather frequent occurrence according to E. Scharrer (personal communication).

The neurosecretory product can be demonstrated between the cells of the corpora cardiaca. The study of preparations stained with Gomori's chrome hematoxylin method suggests also here an arrangement along the nerve fibers. We have never found a trace of the substance stainable with chrome hematoxylin *within* the cells of the corpora cardiaca. The small secretory granules occurring in these elements stain intensely with phloxine (Figs. 4-8).

In the species of which *Chloroperla* represents the type and which possess anatomically well defined nervi corporis allati, the neurosecretory substance is very abundant in these nerves. One can trace it without the slightest difficulty to the corpora allata, and in preparations stained with the Gomori technique its destination can be observed (Figs. 7, 9, 13, 14, 15). The majority of the fibers of the nervus corporis allati, which are neatly outlined by the secretory product, ramify under the connective tissue capsule of each corpus allatum. From these subcapsular plexus, clearly defined by the accumulation of the neurosecretory material, issue fibers also charged with neurosecretory material which ramify between the allatum cells. As in the case of the corpora cardiaca, this product remains extracellular. The transport of the neurosecretory material does not terminate in the corpora allata. The nerves which originate from them and run to the prothorax also contain a greater or less amount of the material stainable with chrome hematoxylin.

In the species whose cephalic endocrine glands belong to the types of *Nemura* and *Brachyptera*, the passage of the neurosecretory product into the corpus allatum appears less pronounced. As a matter of fact, there exists no anatomically defined

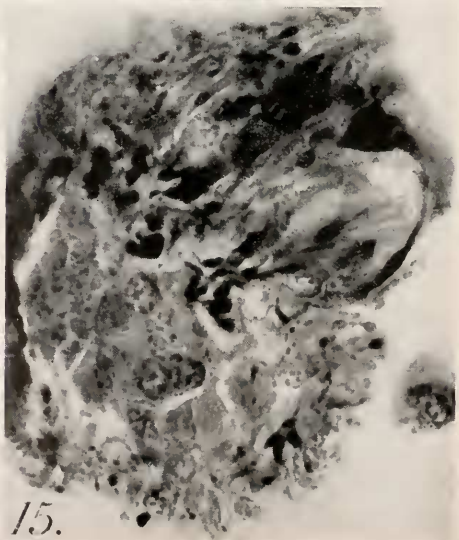
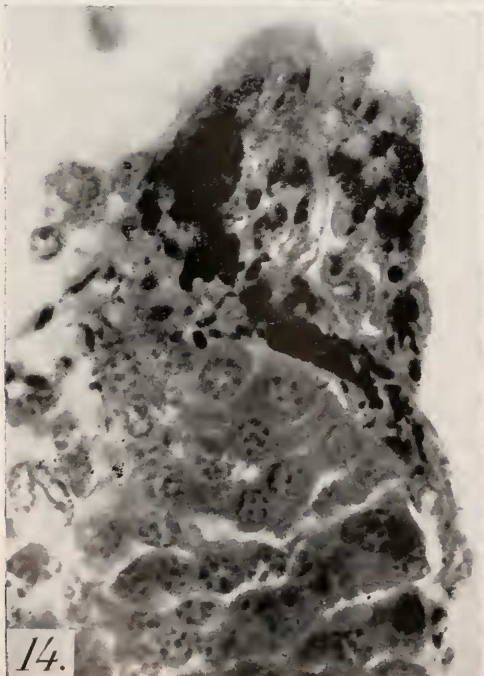
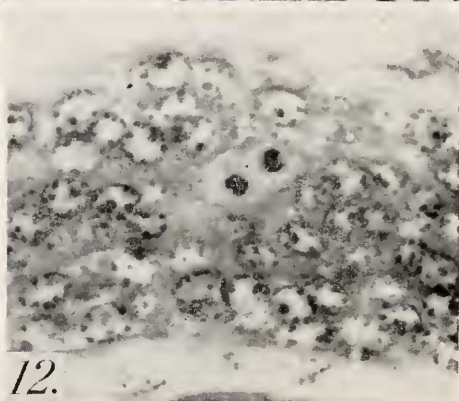
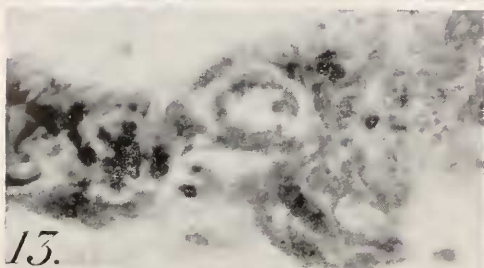
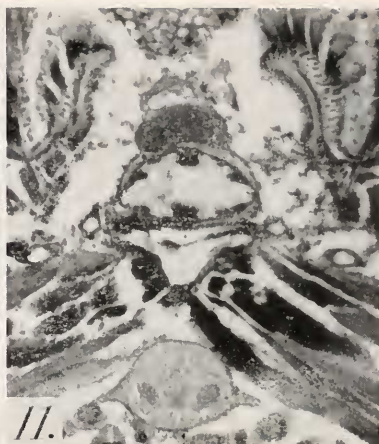
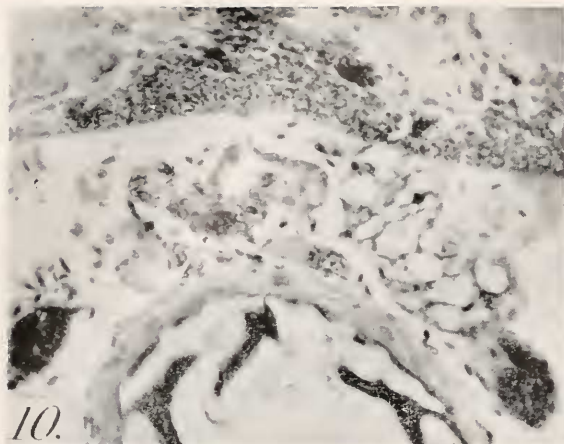
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FIGURE 6. Corpus cardiacum of an old larva of *Perla marginata*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Neurosecretory product between the cells.

FIGURE 7. Frontal section through retrocerebral glandular complex of an old larva of *Nemura murtoni*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Esophageal wall (bottom), corpora cardiaca (above it), and corpus allatum (to the right). Presence of neurosecretory product between the cells of the corpora cardiaca and of the corpus allatum.

FIGURE 8. Frontal section through hypocerebral ganglion and corpora cardiaca of a larva of *Leuctra inermis*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Neurosecretory product between the cells of the corpora cardiaca.

FIGURE 9. Nervus corporis allati and corpus allatum of a young larva of *Perla carlukiana*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Accumulation of neurosecretory product in the nervus corporis allati (top, left) and under capsule of corpus allatum.



FIGURES 10-15.

nervus corporis allati. The corpus allatum is innervated by a certain number of very thin fibers which are accompanied by a substance staining with Gomori's hematoxylin, but which ramify directly among the cells of the corpus allatum without forming a subcapsular plexus, so that there exists no real accumulation of the neurosecretory material. Only the study of sections with very powerful magnifications shows the existence of a phenomenon which, although being less spectacular than in representatives of the type of *Chloroperla*, probably possesses the same physiological significance.

### III. Development of the endocrine glands in the course of post-embryonic life

A comparison of the endocrine glands in various stages of post-embryonic development shows the following facts:

(a) The neurosecretory cells of the pars intercerebralis reach their maximum activity at a stage considerably ahead of the imaginal molt. In the larva whose wing buds are still far from having reached their maximal development one finds the most pronounced transport of neurosecretory substance along the nervi corporis cardiaci and the greatest accumulation of this substance in the corpora cardiaca and allata. The secretory activity of the pars intercerebralis is less noticeable in older larvae and in the imago.

(b) The corpora cardiaca reach their maximal size at a larval stage which corresponds to the maximal secretory activity of the pars intercerebralis. Their volume remains stationary in the older larva and starts to diminish after the adult stage is reached.

(c) The corpora allata develop in the same fashion. Their maximal size falls into the middle of the larval life. During the second half of the post-embryonic period these organs undergo a pronounced atrophy, which is the more clearly visible since it coincides in time with the increase in size of all organs in the head region other than the corpora cardiaca. The size of the corpora allata of the imago is substantially smaller than that of larvae which are about halfway through their post-embryonic development.

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FIGURE 10. Cross section through caudal portion of cerebral ganglion of larva of medium age of *Isoperla grammica*. Dubosq, azan,  $\times 250$ . Fused corpora cardiaca (center) and corpora allata (on either side of upper third of esophagus).

FIGURE 11. Cross section through head of a larva of medium age of *Brachyptera risi*. Carnoy, Prenant's triple stain,  $\times 100$ . Esophagus in center, above it the unpaired medial corpus allatum, above the corpus allatum the common, fused portion of corpora cardiaca.

FIGURE 12. Detail of Figure 11,  $\times 1000$ . Note mitosis in corpus allatum.

FIGURE 13. Nervus corporis allati (at left) and beginning of corpus allatum in an old larva of *Perla marginata*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Note accumulation of neurosecretory product in nervus corporis allati and non-neurosecretory ganglion cell at entrance of nerve into the corpus allatum.

FIGURE 14. Nervus corporis allati and corpus allatum in a larva of medium age of *Perla carlukiana*. Bouin, chrome hematoxylin-phloxine,  $\times 1000$ . Accumulation of neurosecretory product in nerve and subcapsular plexus, as well as in thin fibers penetrating corpus allatum.

FIGURE 15. Nervus corporis allati and corpus allatum of a larva of medium age of *Perla cephalotes*. Technique and magnification as in Figure 14. Note abundance of neurosecretory product in the nerve and between the cells of corpus allatum.

## DISCUSSION

From the anatomical point of view, the differences between the various Plecoptera studied are even more marked than was expected from the work of Hanström (1940). One should perhaps mention here that the anatomy of the endocrine glands is always the same in all representatives of the same family, and that the grouping of the different families according to the morphology of their retrocerebral glandular complex results in an arrangement which is in agreement with present concepts regarding the taxonomy and phylogeny of the Plecoptera.

Concerning the structure of the corpora cardiaca and allata, certain data reported in this paper correspond to facts well established in other insects. Thus, the significance of the connection between the cells of the pars intercerebralis and the corpora cardiaca has been known since Hanström (1940). B. and E. Scharrer (1944) compared this neurosecretory system with the hypothalamic-hypophyseal system of the vertebrates. The newer techniques for the demonstration of the neurosecretory product, in particular the chrome hematoxylin-phloxine method, greatly facilitate the study of this neurosecretory pathway, and the accumulation of the neurosecretory product in the corpora cardiaca described by B. Scharrer (1951) in *Leucophaca maderae*, was confirmed in all insects studied with sufficiently selective methods. We should like to point out in this connection that the use of the chrome hematoxylin-phloxine method permits one to correct an error of interpretation due to the use of unsuitable techniques, i.e., the description of "pseudopodial processes" of the "chromophile cells" of the corpora cardiaca by Cazal (1948). These "processes" are apparently nothing but accumulations of neurosecretory products along nerve fibers.

The existence, in the corpus cardiacum cells themselves, of a second secretory product which differs from that of the neurosecretory cells of the protocerebrum has been debated for a longer time than the accumulation of the glandular product of the protocerebrum. This secretory activity on the part of the corpora cardiaca themselves exists, however, in a variety of insects. It was reported in the Thysanura (Gabe, 1953a), the Ephemeroptera (Arvy and Gabe, 1952a), the Odonata (Arvy and Gabe, 1952b), in *Leucophaca maderae* (B. Scharrer, personal communication), *Carausius morosus* (Stutinsky, 1952), and *Bombyx mori* (Arvy, Bounhiol and Gabe 1953a); the case of the Plecoptera constitutes another example. The particular timing of this secretory process, whose physiological significance was recently discussed by Wigglesworth (1954), explains why its product cannot be as easily demonstrated as the accumulation of the neurosecretory material. In fact, the corpora cardiaca are actively secreting only at well defined periods in the post-embryonic development. Studies, as yet unpublished, showed that the secretory activity of the endocrine glands of the Myrmeleonidae is sharply restricted to certain periods.

Attention should be called to the fact that the existence of two separate secretory products in the corpora cardiaca corresponds to that in other endocrine glands of arthropods. The sinus gland of the crustaceans (Malacostraca) in which the neurosecretory product furnished by the x-organ of Hanström and by other neurosecretory cells of the central nervous system is stored, contains in decapods (Gabe, 1952a) and isopods (Gabe 1952b, 1952c) a second product of secretion. This substance is formed *in loco* and differs from the neurosecretory product in its

chemical constitution. Similarly, the brain gland of the Chilopoda which receives the product of the neurosecretory cells of the protocerebrum contains a second secretory product formed in the cells of the organ themselves and different from the first in its histological and histochemical characteristics (Gabe, 1952d, 1953b). This structural analogy of the three principal neurosecretory systems in arthropods, recently emphasized by one of us (Gabe, 1953c), suggests a comparison with the hypothalamic-hypophyseal system of the selachians (E. Scharrer, 1952): in these the product of the neurosecretory cells of the preoptic nucleus accumulates in the terminals of the hypothalamo-hypophyseal tract between the cells of the intermediate lobe which possesses its own secretory activity.

The transport of neurosecretory material to the corpora allata and its accumulation between the cells of this organ deserves special emphasis because it represents the first example among Heterometabola of a phenomenon recently described in *Bombyx mori* (Arvy, Bounhiol and Gabe, 1953a). The extension of the neurosecretory pathway, which begins in the pars intercerebralis, to the corpora allata speaks in favor of the existence of relationships between the neurosecretory cells of the protocerebrum and the corpora allata (B. Scharrer, 1952; Thomsen, 1952).

The transport of the neurosecretory product in the nerves leaving the corpora allata in the Plecoptera of the Chloroperla type seems to show that the product of the cells of the pars intercerebralis can, in certain cases, reach thoracic organs. This observation is related to the presence of neurosecretory material in the aortic nerves arising from the corpora cardiaca of the Thysanura (Gabe, 1953a), and to the existence of this substance in the esophageal nerve of *Calliphora erythrocephala* (Thomsen, 1954).

The study of the post-embryonic development shows that the relations of the corpora cardiaca and allata to the neurosecretory cells do not merely represent an anatomical peculiarity. The maximal size of the corpora cardiaca and the onset of their own secretory activity coincide with the maximal abundance of the neurosecretory product between the cells and the appearance of numerous vacuoles in the cells of origin of the nervi corporis cardiaci I. The largest size of the corpora allata is reached at the same time and seems to be correlated with the arrival of the neurosecretory product.

The development of the corpora cardiaca throughout the post-embryonic life of the Plecoptera is very different from that reported for other insects. The corpora cardiaca reach their maximal size at the time of the imaginal molt in Ephemeroptera (Arvy and Gabe, 1950, 1952a), in Odonata (Arvy and Gabe, 1952b), and in *Panorpa communis* L. (Schwinck, 1951), during pupation in *Ephestia kühniella* Zell. (Rehm, 1951) and in *Bombyx mori* (Arvy, Bounhiol and Gabe, 1953a, 1953b). This difference in development whose physiological significance cannot be determined except by experimentation seems to correspond to a difference in timing regarding the neurosecretion in the protocerebrum. We could show a time relationship between the maximal transport of the neurosecretory product and the maximal size of the corpora cardiaca in the Ephemeroptera and Odonata (Arvy and Gabe, 1952a, 1952b, 1953a). The same agreement exists in *Ephestia kühniella* as shown by the measurements and descriptions of Rehm (1951). Finally, in *Bombyx mori* the increase in the volume of the corpora cardiaca takes place at the same time as a "discharge" of the neurosecretory product of the cells of the pars intercerebralis (Arvy, Bounhiol and Gabe, 1953a, 1953b).

The development of the corpora allata shows the same feature. The maximal size of these organs corresponds, in the Plecoptera, to a larval stage still far from the imaginal molt; these organs undergo atrophy in the second half of post-embryonic development. In other insects whose corpora allata are innervated by the protocerebrum the maximal size is reached in the imago. It coincides with an intense secretory activity in the cells of the pars intercerebralis. In the Ephemeroptera, the corpora allata develop as in the Plecoptera. Their maximal size is also reached towards the middle of the post-embryonic period, and the atrophy which follows corresponds to a reduction of secretion in the cells of origin of the nervi corporis allati lying in the subesophageal ganglion in the Ephemeroptera, and in the pars intercerebralis in the Plecoptera.

In general, the study of the modifications which the endocrine glands of the head region of the Plecoptera undergo during post-embryonic life illustrates the parallelism between the state of the endocrine glands and the secretory activity in the cells of origin of the nerves which innervate these organs. This fact underlines the important role of the neurosecretory phenomena in the physiology of these insects.

#### SUMMARY

The histophysiological study of the intercerebralis-cardiacum-allatum system in 21 species of Plecoptera resulted in the following observations:

1. From the anatomical point of view, the type of *Chloroperla* (Hanström, 1940) characterized by paired symmetric corpora allata, exists in the Perlodidae, Perlidae, and Chloroperlidae. The type of *Nemura*, characterized by an unpaired, laterally located corpus allatum, corresponds to the Nemuridae, Leuctridae, and Capniidae. A third anatomical type of which an unpaired but definitely medial corpus allatum is typical (type of *Brachyptera*) exists among the Taeniopterygidae.

2. The cells of origin of the nervi corporis cardiaci I of the Plecoptera possess all the morphological characteristics of neurosecretory cells. Their secretory product is stainable with acid dyes, azocarmine, iron hematoxylin, and chrome hematoxylin. This secretory product migrates along the axons and accumulates between the cells of the corpora cardiaca. These elaborate a secretory product of their own which stains with the phloxine of the method of Gomori.

3. The neurosecretory product migrates along the nervi corporis allati and occurs between the cells of the corpora allata; one also encounters it in the nerves which run from the corpora allata to the prothorax in the Plecoptera of the *Chloroperla* type.

4. The secretory activity in the cells of the pars intercerebralis is at its peak towards the middle of the larval period; the phenomena of neurosecretion are less pronounced in the later stages of larval life and in the imago.

5. The corpora cardiaca and allata reach their maximal volume in larvae which are still a considerable period away from the imaginal molt. In the latter stages of post-embryonic development atrophy of the endocrine glands of the head region is observed. This mode of development is different from that described in other insects belonging to the Neoptera; it must be understood in relationship with the peculiar chronology of the neurosecretory activity of the Plecoptera.

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